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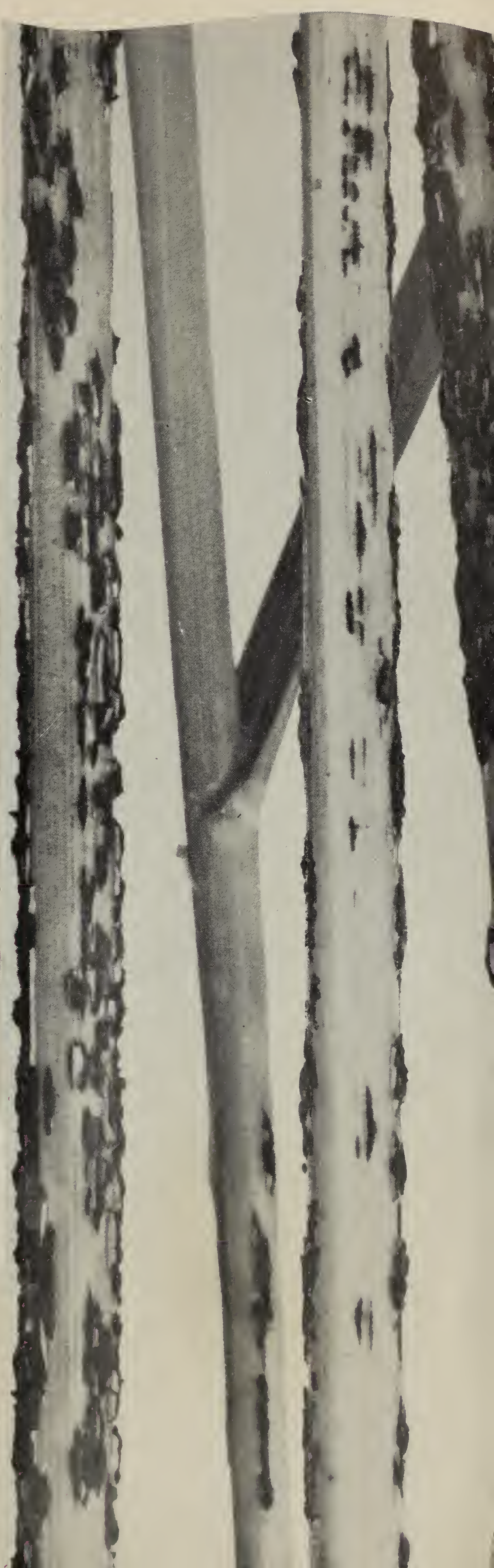

STEM RUST of CEREALS

BY
J. H. CRAIGIE

BOTANY AND PLANT PATHOLOGY DIVISION

CANADA DEPARTMENT OF AGRICULTURE, OTTAWA, ONTARIO

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STEM RUST OF CEREALS

J. H. CRAIGIE

INTRODUCTION

Stem rust is a disease of wheat, oats, barley and rye, as well as of a number of different grasses. It occurs in practically every region where cereals are grown. One or two of the other five cereal rusts may occur at the same time on the same crop plant. For instance, stem rust and leaf rust very commonly occur together on wheat, which in some regions is subject to stripe rust as well. Similarly, stem rust, dwarf leaf rust, and stripe rust may be present on barley. Crown rust may be present on oats, or brown leaf rust on rye, at the same time as stem rust. Wherever prevalent, each of the other rusts causes a greater or less amount of damage, and in some regions or localities the damage from stripe rust or crown rust or from one of the leaf rusts may be greater than that from stem rust. Of all the cereal rusts, however, stem rust is the one most universally dreaded. The loss from it far exceeds that from any of the others.

Some idea of the enormous losses caused by this disease may be gained from the estimated damage done to the wheat crop in three of the north-central States (Minnesota, North Dakota, and South Dakota) and in Western Canada. In 1916 alone, the loss in these two areas was estimated at 180,000,000 and 100,000,000 bushels, respectively. In the three States mentioned above, the average annual loss from 1916 to 1922 was estimated at 44,000,000 bushels. During the years from 1925 to 1935, the average loss in Manitoba and Saskatchewan has been calculated to be about 35,000,000 bushels, or nearly 11 per cent of the possible yield. These estimates are for yield alone, and do not take into consideration the very appreciable loss in the value of the crop due to reduction in grade and quality.

Because of the great economic importance of the crops affected, stem rust has been the subject of investigation in many countries. Much information has been brought to light concerning its cause, its method of spread, and the environmental factors that favor or retard its development. In recent years, attention has been given to controlling stem rust and notable progress has been made, particularly in the direction of producing resistant varieties of cereals.

Canadian rust investigations, and the work on breeding for rust resistance, have been carried on, for the most part, at the Rust Research Laboratory established at Winnipeg by the Canada Department of Agriculture in 1925. In 1938 the laboratory was divided into two sections designated as the Plant Pathology Laboratory, and the Cereal Breeding Laboratory, and the original name, Rust Research Laboratory, was discontinued.

The Canadian universities, in particular the Universities of Manitoba, Saskatchewan, and Alberta, have engaged at various times in rust research and have made valuable contributions in both plant breeding and rust pathology. Some of these investigations have been supported by grants from the Canada Department of Agriculture and the National Research Council. Throughout the years there has been close collaboration between Canadian rust investigators and those in the United States, Mexico, and certain Commonwealth countries.

The distribution of rust-resistant wheats in Canada began in 1936, and by 1938 somewhat more than half the wheat acreage in Manitoba was sown to resistant varieties. By 1939 these wheats were being widely grown in eastern Saskatchewan. It has been estimated that the growing of resistant wheats in the rust area of Manitoba and eastern Saskatchewan over the period 1938-1943 increased the average annual wheat production of that area by about 41,000,000 bushels. Rust-resistant varieties of oats were also distributed in Western Canada in 1936 and soon became widely grown in the area affected by oat stem rust.

As a result of the extensive growing of resistant varieties of wheat and oats, damage from stem rust in Western Canada was reduced almost to insignificance during the decade 1940-1950. In more recent years, and especially since 1950, changes in the rusts have taken place that have enabled them to overcome the resistance of the new varieties to the extent that losses from stem and leaf rust of wheat, particularly in 1954, were comparable to losses sustained in the years before the production of rust-resistant varieties. The nature of these changes and the countermeasures taken by plant scientists are outlined in the section on plant breeding.

HISTORY OF STEM RUST

How far back in the history of agriculture stem rust first began to do damage to cereal crops, no one can say. It is known, however, that "rust" was destructive to such crops in Greece and Italy two or three hundred years before the beginning of the Christian Era. Other cereal rusts may have been included under this name, but the likelihood is that a good part of the damage was done by stem rust. The disease has probably been present in southern Europe ever since that time. It has been causing damage in northern Europe for two or three centuries at least. It was probably present in Asia long before the time of the Greeks and Romans. Some authorities are of the opinion that the "blasting" and "mildew" mentioned in the Old Testament (for example I Kings 8: 37; II Chron. 6: 8; Haggai 2: 17) refers, at least in part, to stem rust. Others are inclined to question that opinion. Undoubtedly the disease is a very ancient one.

Little is known of how or when the disease became distributed throughout the world. A severe outbreak of stem rust occurred as early as 1703 in South Africa. It was causing serious damage in the New England States about the same time. It appeared in Australia not long after the cultivation of wheat was undertaken there, the first heavy attack occurring in 1803. It was found in South America before the opening of the present century, but it was probably there much earlier. For the last 65 years, and probably for centuries before, it has been a serious menace to wheat production in India.

With regard to Canada, it is probable that stem rust began to attack the crops in what is now the provinces of Quebec and Ontario fairly early in the agricultural history of these provinces. About the middle of the last century one writer stated that there was "nothing the Canadian farmer suffered so much from as rust in their wheat crops." From his account, there is little doubt that he refers mainly to stem rust. He does not state how long before that time rust had been causing serious losses to Canadian farmers, but it is plainly evident from his statement that the disease had been troublesome for many years and that farmers and others were earnestly endeavoring to find some means of controlling it. At that time, and even much later, the popular belief was that certain climatic and soil conditions caused the crops to rust, although about 50 years earlier the parasitic nature of the disease had been definitely established.

The first record of its occurrence in Western Canada seems to be that of Dr. John Dearness, who, while on a visit to Manitoba in the summer of 1891, found it at several points in that province. There is little doubt that it was present previous to that year. From what is known concerning the spread of the disease and its occurrence in the Mississippi Valley, there is a possibility at least that stem rust was present on the wheat crop from which the first export shipment was made from Manitoba in 1876. In those earlier years it was apparently of no great importance.

In the Report of the Dominion Experimental Farm, Brandon, Man., for 1896, Dr. Bedford, the Superintendent, records that the months of April and May, were wet and temperatures for May were from 3° to 6° F. above average. On June 27 the crops began to lodge, and a few days later rust attacked the stems of wheat and oats. Temperatures and rainfall in July, August, and September were about average for those months, "but in spite of this," he says, "the ravages of rust continued, and were shown in delayed ripening, rusty weak straw, shrunken heads, reduced yield and a light weight sample". There is no doubt that the rust referred to in his report was stem rust. In 1897, on the other hand, there was "almost a total absence of rust among grain crops". "Rust" was therefore recognized at that time as being injurious to cereal crops in Manitoba, although it is apparent from the reports that stem rust was not distinguished from any of the other cereal rusts.

The year 1916 is generally regarded as the first bad "rust year," and undoubtedly stem rust was more destructive in that year than in any previous one. It was, however, by no means altogether absent from Western Canada in the earlier years of this century. In 1902, Dr. Bedford states in his report that "this disease (rust) is one of the chief factors in reducing the yield of wheat, especially during seasons of abundant rainfall such as we have had during the last two years." Rust was "very prevalent on the stronger soils" in the district around Brandon in 1903 and, on the Farm, both the "yield and sample were greatly injured, especially on valley land". The Superintendent of the Dominion Experimental Farm, Indian Head, Sask., reported that in 1902 rust "hitherto almost unheard of in the Territories" did a small amount of damage, and that on the Farm in 1903 a number of varieties were "struck by rust." In the latter year wheat on fertilizer plots was so badly rusted that the yield data were of no use. Stem rust was severe enough in 1904 to cause widespread alarm and rather heavy loss in Manitoba and in Saskatchewan (then a part of the Northwest Territories). It was fairly prevalent in 1905. In 1911 it did considerable damage in western Manitoba and eastern Saskatchewan, where cold wet weather during August delayed ripening of the wheat crop.

The years from 1900 to 1939 may be divided into light-, medium-, and heavy-rust years, according to the severity of stem rust on wheat in Western Canada. The heavy-rust years are 1904, 1916, 1923, 1927, 1935, and 1938, the worst ones being 1916 and 1935. In the medium-rust years, 1911, 1919, 1921, 1925, 1930, and 1937, infection was somewhat less severe and usually involved a less extensive area. The years not classed as heavy- or medium-rust years may be regarded as light-rust years. During the first half of the period under review, the information concerning the prevalence of the disease is generally scanty, and it may be possible that certain years, for example 1903 and 1905, should be classed as medium- rather than as light-rust years.

From 1940 to 1949, because of the widespread cultivation of rust-resistant varieties, little damage from rust occurred. Following a rather sudden change in the parasitic behavior of wheat stem rust in 1950, slight damage was done to bread wheats in 1951 and 1952, moderate damage in 1953, and severe

damage in 1954. In this period, the formerly rather rust-resistant durum wheats were far more susceptible than the bread wheats and, in 1952 and 1953, and especially in 1954, durum wheats suffered heavy rust losses.

CAUSE OF STEM RUST

Stem rust is caused by a fungus. The other cereal rusts are caused by other closely related fungi. Fungi are plants, but, unlike ordinary plants, they do not possess green coloring matter in their cells and hence they are unable to manufacture their own food. On this account, they must obtain their food ready-made. Some of them can attack living plants or animals and procure

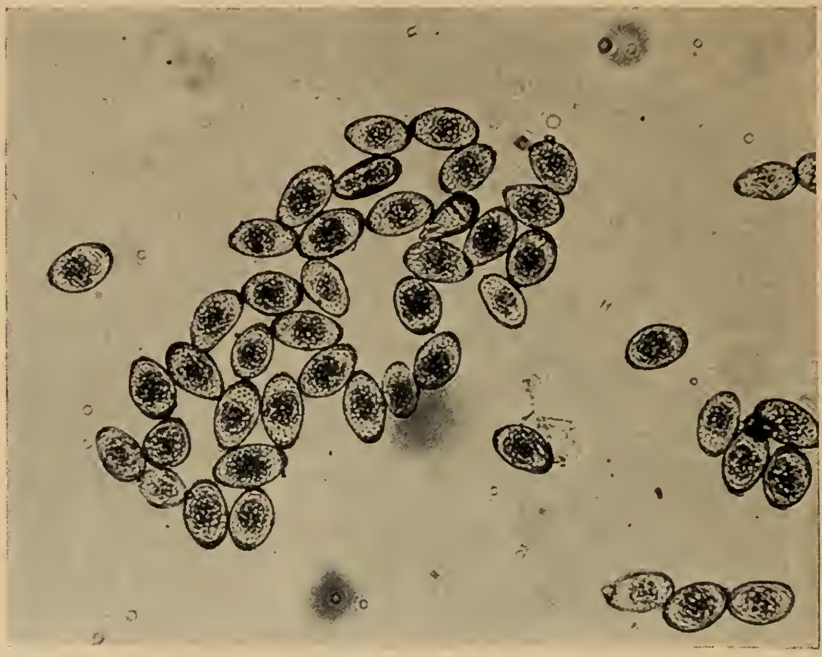

Figure 1.—Red spores (urediospores) of stem rust. Notice their egg-shaped appearance, also the denser color of their centers due to the presence of a reddish coloring substance in oil globules collected there. Magnification, 230 app. (Photograph by Mr. A. M. Brown)

their food from them. Such fungi are known as parasites. Others are able to feed on dead matter, and are known as saprophytes. The fungus causing stem rust (*Puccinia graminis* Pers.) is a parasite and obtains its food from green plants, some of which have already been mentioned. As a matter of fact, all of the rust fungi are strictly parasitic.

In the course of its development, the stem-rust fungus appears on its hosts in three different guises, usually referred to as "stages" of the fungus. Two of these stages, the red (uredial) stage and the black (telial) stage, occur on cereals and grasses. The red stage is the one present on such plants while they are green, and on this account is often spoken of as the summer stage. It appears as red spots, or pustules, chiefly on the stems and leaf sheaths, but sometimes on the leaves. The pustules owe their color to the spores (Figure 1) produced in them, which, in mass, are red. The black stage (Figure 2) appears when the infected plants begin to ripen. This is the stage that is present at harvest time, and from it the disease sometimes gets the name "black rust". In this stage, the spores (Figure 3) are dark brown or black. The third stage (Figure 4) occurs on species of barberry, particularly the common barberry. No other species has been so widely and frequently associated with the outbreaks of stem rust. The three stages just mentioned constitute the chief divisions in what is known as the "life cycle" of the fungus. In it the common barberry plays an extremely important part.

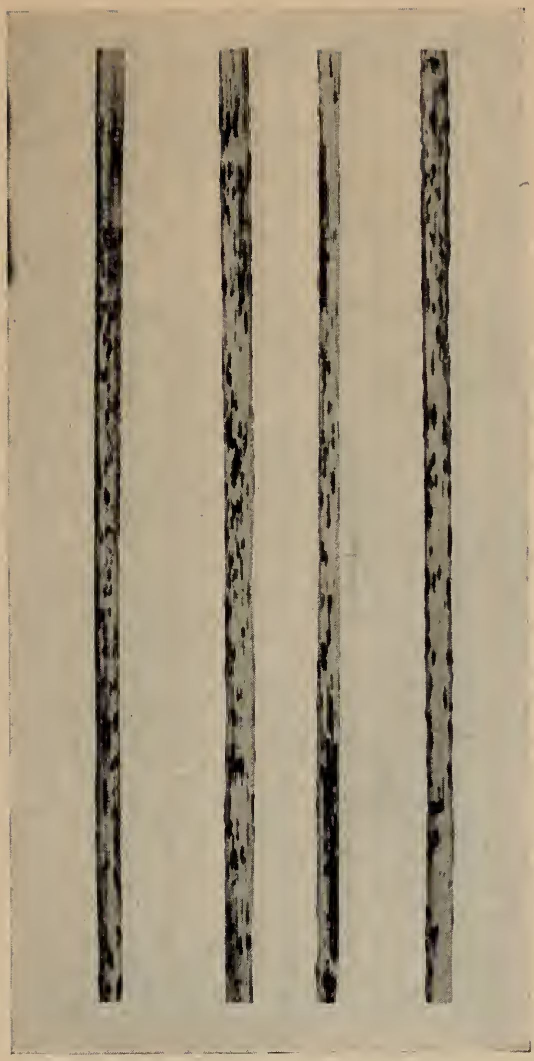

Figure 2.—Portions of wheat stems showing pustules of stem rust in the black (telial) stage. (Photography by Mr. A. M. Brown)

Figure 3.—Black spores of stem rust. Notice that they are two-celled and that the cell-wall of each spore is much thickened toward the tip. Magnification, 240 app. (Enlarged somewhat, after Bailey)

THE COMMON BARBERRY

The common barberry is a shrub (Figure 5), much used in recent times for hedges and other ornamental purposes. Formerly it was cultivated for its berries, from which jellies and wine were made. Under favorable conditions, it may grow to a height of 10 or 12 feet. The leaves, either green or purplish, occur in small clusters of three or more. At the base of each cluster there is

Figure 4.—Under side of a barberry leaf heavily infected with stem rust. Aecia have developed in most of the infections. Somewhat enlarged. (Photographed by Dr. D. L. Bailey)

usually a three-pronged spine, which in reality is a much-reduced leaf. The margins of the leaves are saw-toothed, each tooth ending in a short sharp bristle (Figure 6). The small yellow flowers are arranged in loose drooping clusters. The berries are scarlet, and they remain attached to the plant long into the winter.

This shrub is not a native of North America. Probably its native home is Central Asia. It seems to have been introduced into southern Europe by the Arabs in the seventh century, but apparently was not planted to any great extent in northern Europe until about the seventeenth century. It was brought to America by the early colonists, and eventually became naturalized in the New England States. As settlement progressed westward, the shrub became rather widely distributed through the Middle-Western States. Here, to some extent, it escaped from cultivation. It does not appear to have been so extensively introduced into other parts of the United States.

Little is known about its early introduction into Canada. Probably in Eastern Canada some plantings were made fairly early. A bulletin issued in 1888 by the Ontario Agricultural College advised farmers against the planting

of barberry. Evidently it had been planted to some extent in rural communities before that time. Its introduction into the Prairie Provinces was limited, and probably occurred mostly in the early years of this century. It was probably introduced into British Columbia about the same time.

The common barberry (*Berberis vulgaris* L.) should not be confused with the Japanese barberry (*Berberis thunbergii* DC.), a shrub immune to stem rust. The Japanese barberry is a low spreading shrub, having smooth-edged leaves and usually a single spine at the base of the leaf cluster.

Long before the exact relationship between common barberry and stem rust was discovered (1864-65), farmers had observed that grain in the neighborhood of this shrub was usually a failure. Between 1726 and 1766, three of the New England States (Connecticut, Rhode Island, and Massachusetts) enacted laws for its eradication. From 1800 onward, different countries of Europe passed similar legislation. Following the severe epidemic of stem rust in 1916, the common barberry was outlawed in thirteen of the north-central States and in the Prairie Provinces, and its eradication was undertaken.

Figure 5.—A common barberry bush, the "alternate host" of stem rust. On it develops the spring, or cluster-cup stage of the fungus. (Courtesy of the United States Department of Agriculture)

LIFE CYCLE OF THE FUNGUS

An account of the life cycle of the stem rust fungus may be conveniently begun at the red stage of the cycle. Suppose that one of the red spores (urediospores) lodges on a green wheat plant as it grows in the field. So long as the

plant remains dry, the spore cannot germinate and, therefore, cannot infect the plant; but if a film of moisture—either of dew or rain—covers the plant, the spore germinates (Figure 7) within an hour or two, and sends out a rootlike process, called a germ tube, which enters the plant through one of its numerous breathing pores (stomata). Once the tip of the germ tube is well inside the breathing pore, outside moisture is no longer necessary, for the germ tube is then able to make use of the water in the plant itself.

The tip of the germ tube soon begins to branch, and within a few days a system of rootlike fungus threads, called a mycelium, penetrates between the cells of the plant, just around the spot where the germ tube first entered. These threads send out suckers (haustoria) that are able to pierce the walls of the plant cells and feed on the plant food within the cells. After four or five days, a new development begins. Just beneath the epidermis, or outer covering layer of the plant, the mycelium begins to produce young spores at the ends of stalklike cells that point outwards towards the epidermis. As growth of the spores and mycelium proceeds, the pressure beneath the epidermis becomes too great and the epidermis ruptures, exposing a mass of red spores. Around the margin of the pustule thus formed can usually be seen the ragged edge of the ruptured epidermis. Figure 8 shows a cross section through such a pustule.

Figure 6.—A young twig of the common barberry. Notice the saw-toothed edge of the leaf and the three-pronged spine at the base of each group of leaves. About one-third natural size. (Photograph by Mr. A. M. Brown)

In ordinary summer weather, this whole development, from the entry of the germ tube to the eruption of the pustule, requires about seven or eight days. The spores readily become detached from the stalk cells on which they

are produced, and are easily carried by winds to other plants where, as soon as weather conditions are favorable, they germinate and cause new infections. A single spore, after it infects a plant, may thus give rise in the next generation to several hundred other similar spores. As long as the crops remain green and weather favorable, this process of infection and multiplication of spores continues. In due course, however, the crops mature and ripen. Further infection can no longer take place, and the spread of the disease is over for that particular season.

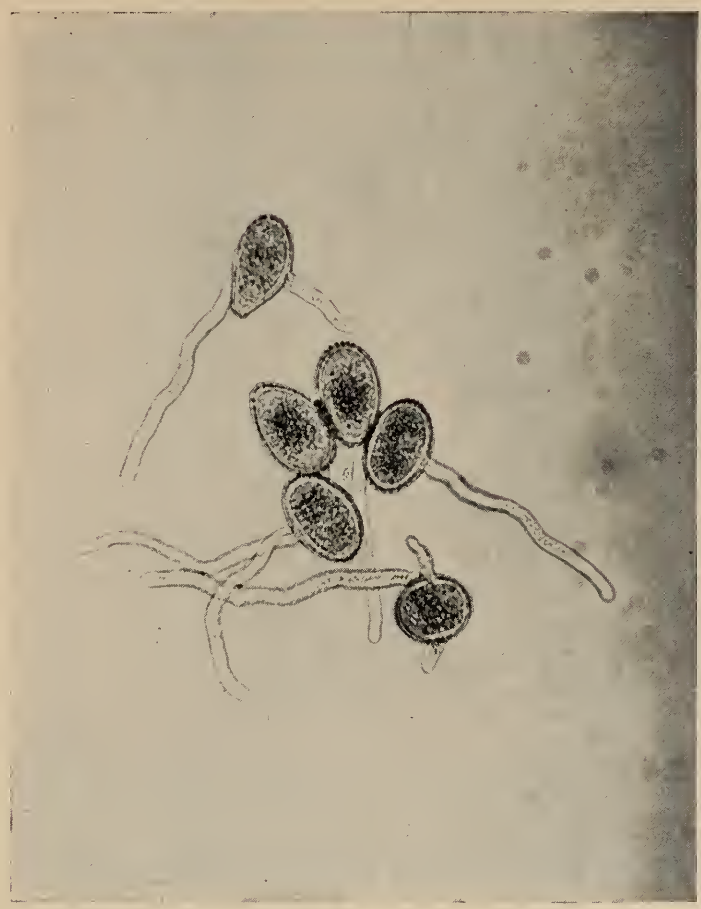

Figure 7.—Germinating red spores (urediospores) of stem rust, showing the germ tubes growing out from the spores. The germ tubes enter the breathing pores of cereal plants and thereby infect them. Magnification, 300 app. (Photomicrograph by Mr. A. M. Brown)

While the plants are ripening, however, a peculiar change takes place in the pustules. As stated earlier, the pustules cease to produce red spores (urediospores) and in their stead produce black ones (Figure 9). After their formation, the black spores (teliospores) enter a dormancy period which lasts for upwards of six months. They pass most of the winter in this state, hence they are often called winter spores. When moisture and warmth return in the spring they readily germinate. They are two-celled, have a dark-brown wall much thickened at the spore tip, and remain firmly attached to the stalk cells on which they are produced (Figure 10). They are not, therefore, adapted for distribution by the wind, as are the red spores. In fact, their distribution would be of little or no value to the fungus, even if green crops were present, for these black spores, unlike the red ones, are quite incapable of infecting any cereal or grass.

The germination of the black spore is different from that of the red spore. Each cell of the black spore sends out a rather short stoutish curved tube which in turn produces four small conical projections (sterigmata), arranged

along the outer side of the curve, towards the end of the tube. At the tip of each of these four projections is produced a very small colorless spore (Figure 11). These tiny delicate spores (sporidia) form very rapidly, in 20 to 25 minutes, and almost immediately afterwards they are shot off into the air and are carried away by currents of air. Eventually they either sink to the ground or lodge on plants of one kind or another. They cannot infect cereal plants, but if any of

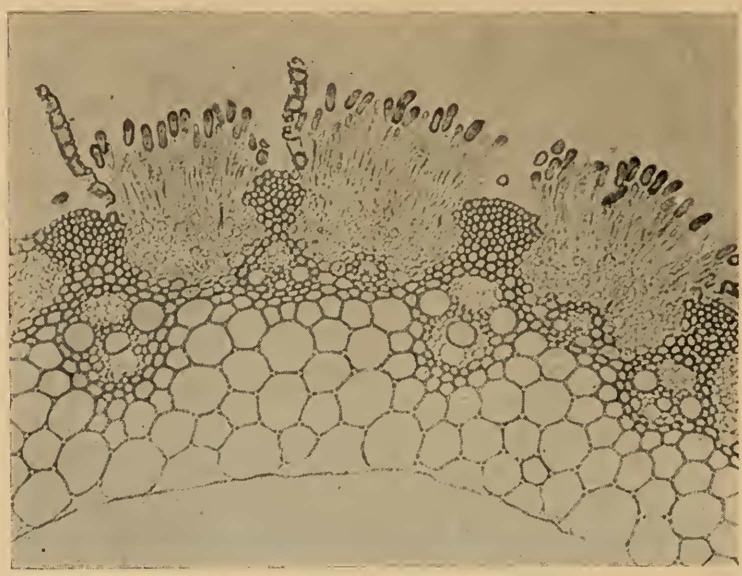

Figure 8.—Cross section through a wheat stem, showing pustules of stem rust in the red stage, with the urediospores borne on their stalk cells. Notice that the mycelium develops in the thin-walled green tissue between the thick-walled woody bundles. The ruptured epidermis can be seen thrown back at the left of two of the pustules. The spores are somewhat collapsed by the fixing treatment. Magnification, 90 app. (Photomicrograph by Mr. A. M. Brown)

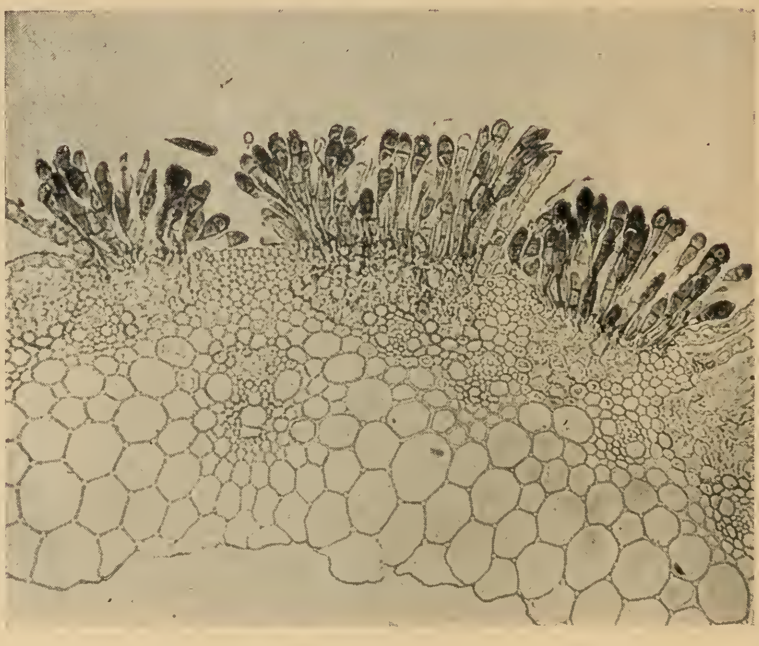

Figure 9.—Cross section through a wheat stem, showing pustules of stem rust in the black stage. Notice that the outer layer of plant cells, the epidermis, has been burst open and thrown back, and is visible at the margin of the pustules. The black stage follows the red stage and hence develops in the same thin-walled tissue between the thick-walled woody tissue. Magnification, 90 app. (Photomicrograph by Mr. A. Mr. Brown)

them happen to fall on young leaves of barberry (and a film of moisture is present on the leaves) they germinate. On germination, each spore produces a sharp peglike tube that punctures the leaf surface. Thus the fungus gains entrance to the inside tissue of the leaves, and there begins to grow, much in the same way as it did after the red spore germinated and entered the wheat plant.

Figure 10.—Section through a pustule of stem rust, showing the black spores supported on their long stalk-cells, from which the spores are not easily dislodged. Magnification, 180 app. (Photomicrograph by Mr. A. M. Brown)

Figure 11 —A drawing to represent the germination of a black spore. The top cell has produced a promycelium on which have been developed four sporidia, borne at the tips of the sterigmata. One spore has been shot off into the air and one is only partially developed. Usually the sporidium nearest the spore matures last.

Within five or six days after infection has occurred, small circular spots appear on the leaves, and in the next week or two these spots, or pustules, enlarge and may reach a diameter of from an eighth to a quarter of an inch, sometimes more. The mycelium in the leaf tissue of each pustule gives rise, on the upper side of the leaf, to a number of vase-shaped structures called pycnia (Figure 12). Usually some pycnia occur on the underside also. In the pycnia are produced extremely small spores (pycniospores) and a honeylike fluid, called nectar. The function of the pycniospores is described in detail on page 25.

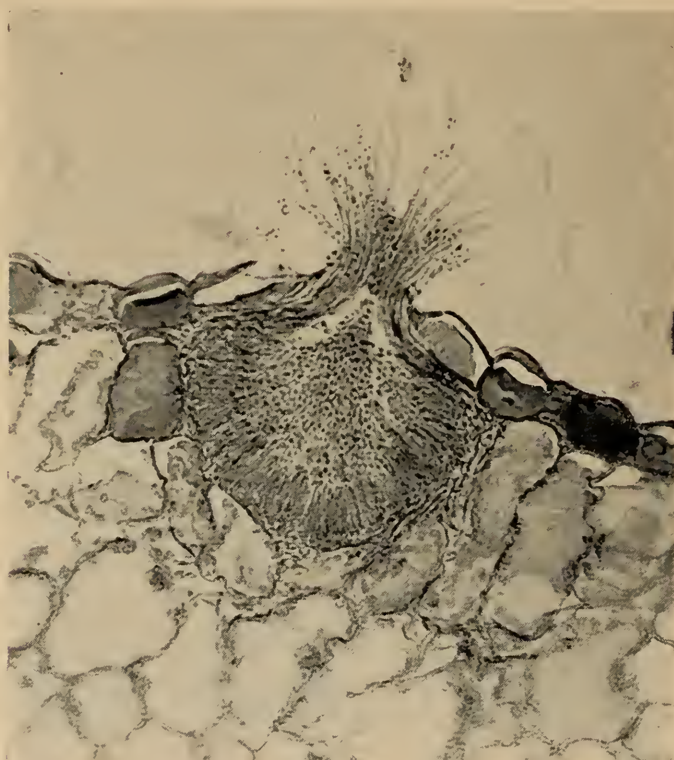

Figure 12.—Part of a cross section through a stem-rust infection on a barberry leaf, showing a pycnium opening to the upper side of the leaf. Notice the brush of hyphae, or threads, projecting through the mouth of the pycnium. A mass of the minute pycniospores is seen at the center of the cavity, and, around the inside wall, can be seen the short parallel hyphae, at the tips of which the pycniospores are produced. These spores flow out through the mouth of the pycnium, carried by the nectar produced in the pycnium. Magnification, 350 app.

Projecting through the opening at the top of each pycnium is a brush of fungus threads. These threads are of two types. In one type, they are awl-shaped and stiff; in the other they resemble, and are probably the same as, the fungus threads within the leaf tissue. Those of the second type are longer and less rigid than those of the first type, and occasionally are branched. The nectar and the pycniospores ooze out through the opening in the top of each of the pycnia and collect on the upper surface of the pustule.

On the underside of the pustules, structures of a different kind are formed. These structures are generally referred to as cluster cups (Figure 13). They are tubular in shape and are packed full of spores arranged in parallel chains (Figure 14). The cups are called aecia and the spores, aeciospores. The aecia open at the exposed ends, and the aeciospores are shot into the air and are carried away by wind. However, the aeciospores cannot infect barberry, but if they happen to reach green plants of some susceptible cereal or grass (and moisture conditions are favorable), they infect them. Infections by these spores give rise to the red, or summer, stage of the fungus, thus completing the life cycle. The relation of the pycnia to the aecia is shown in Figure 15.

In regard to the production of aecia and aeciospores by pustules on barberry, it may be mentioned that they arise as a result of a sexual process. This aspect of the life cycle can, however, be more conveniently discussed in a later section which deals with hybridization in stem rust.

Briefly stated then, the life cycle (Figure 16) of the stem-rust fungus has three principal stages: (1) the red, or summer, stage in which the disease spreads from one cereal plant to another; (2) the black, or winter, stage in which the fungus passes the winter in a dormant condition; and (3) the cluster-cup, or spring, stage which occurs on barberry and which serves as a link between the black stage of one year and the red stage of the following year.

Figure 13.—Cluster cups (aecia) on the underside of a pustule of stem rust on a barberry leaf. Magnification, 8 app. (After Bailey)

PHYSIOLOGICAL SPECIALIZATION

Varieties of Stem Rust

There are several different varieties of stem rust. One variety attacks wheat and barley, but does not attack oats. Another attacks oats, but not wheat or barley. A third occurs commonly on rye. It can infect barley, but not wheat or oats. For convenience these three varieties are generally referred to, respectively, as wheat stem rust, oat stem rust, and rye stem rust. Each of them attacks certain grasses. For example, wheat stem rust is very common on wild barley, and rye stem rust on couch, or quack, grass. Then again there are other varieties of stem rust that do not attack cereals, but occur on particular kinds of grasses. One of these attacks timothy, another attacks species of *Agrostis*, and still another, species of *Poa*.

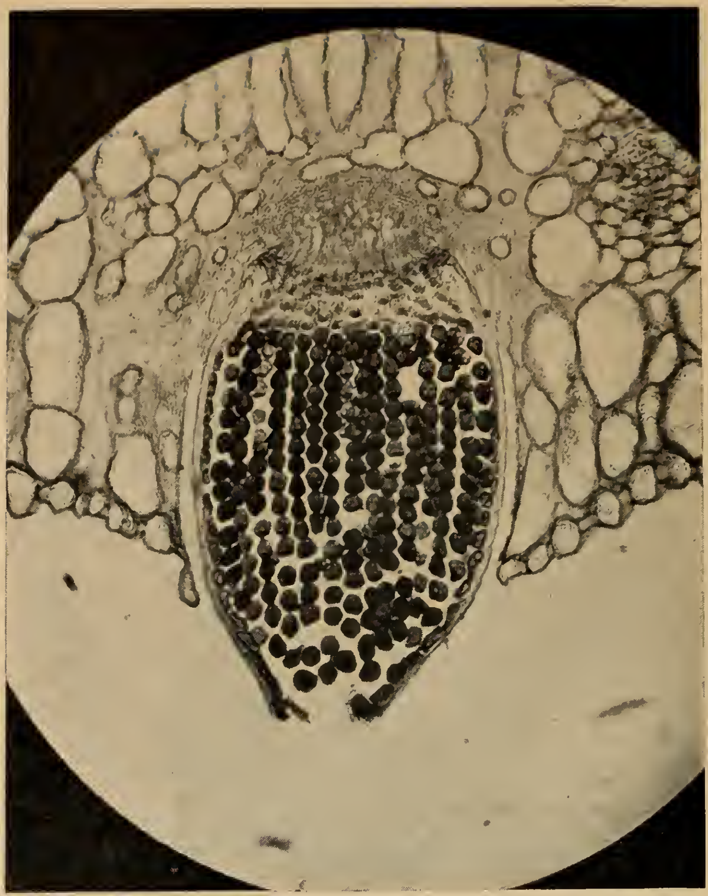

Figure 14.—A section cut lengthwise through a cluster cup (aecium) of a stem-rust pustule on a barberry leaf. Observe that the aecium is only partly open at the exposed end and that the aeciospores are produced in parallel rows, the youngest ones being farthest from the exposed end of the aecium. (The spores have been considerably disturbed and the rows broken by the sectioning process.) Magnification, 120 app. (Photomicrograph by Mr. A. M. Brown)

Figure 15.—A cross section through a pustule of stem rust on a barberry leaf, showing a pycnium on the upper side and aecia on the lower side. Fungus threads, or hyphae, penetrate between the cells of the leaf in all directions, and connect the pycnium with the aecia. Many pycnia besides the one shown were present in the pustule. Magnification, 90 app. (Photomicrograph by Mr. A. M. Brown)

All the varieties look much alike, though the urediospores of the varieties that attack the above-mentioned grasses are somewhat smaller than those of the varieties that attack cereals. But although alike in appearance they are actually quite different because they do not usually attack the same cereal or grass hosts. The difference between them lies in their physiological, or constitutional, make-up. Hence they are called physiological varieties, and are said to be physiologically specialized to their respective hosts.

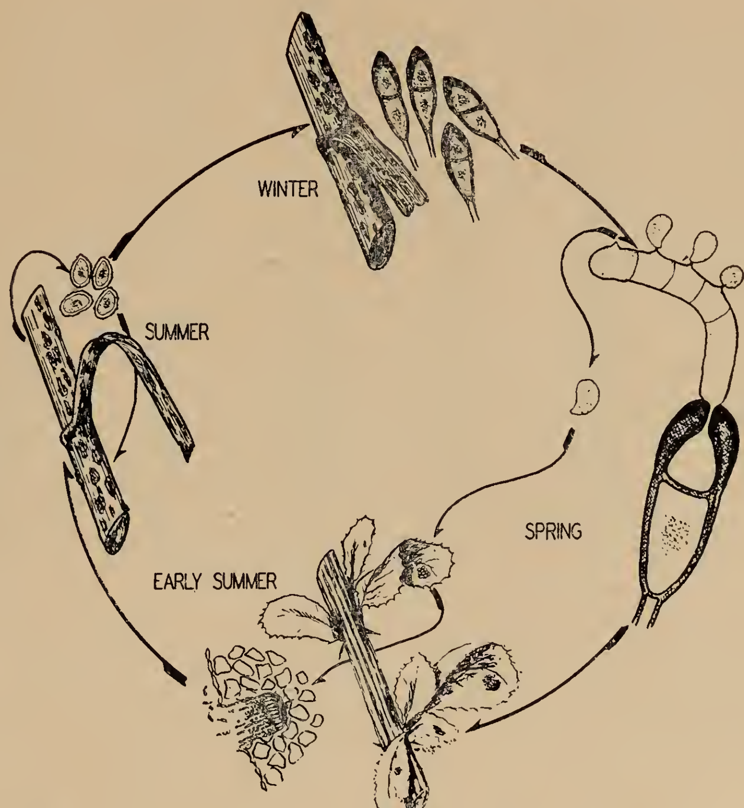

Figure 16.—A schematic representation of the life cycle of the stem-rust fungus. During the summer, the red spores infect green crops. When the crops begin to ripen, black spores are produced. They survive the winter and germinate in the spring. On germination, they produce sporidia, which infect barberry. The infections give rise to the cluster-cup spores, which, in turn, infect cereals and grasses. (Drawn by Mr. W. E. Clark)

Races of Stem Rust

Specialization occurs also in the varieties themselves. The varieties are, therefore, said to be composed of physiologic forms or, as they are presently known, physiologic races. Over 230 races have been distinguished in wheat stem rust, although only 14 have been differentiated in oat stem rust and 14 in rye stem rust. In each of these three varieties of stem rust, the physiologic races are distinguished by the types of infection which each race produces on seedlings of a given set of cereal varieties. For identifying or distinguishing races of wheat stem rust, twelve different standard varieties of wheat are used; for races of oat stem rust, five varieties of oats; and for races of rye stem rust, five varieties of rye. The differential varieties are sometimes called differential hosts.

The types of infection are shown in Figure 17. They vary from whitish flecks in which no spores are produced to large pustules in which there is an abundance of spores. Each type is represented by a symbol. The 0-type represents immunity—the complete absence of any evidence of infection, the 4-type represents very high susceptibility. Actually in the figure, the 0-type is not shown, but in its place a type showing flecks (0;) is substituted. The

flecks indicate that infections occurred and killed groups of cells at a number of points. As the fungus cannot feed on dead tissue, it was unable to develop further and hence failed to produce any spores. The intermediate types, 1, 2, and 3, represent increasing susceptibility between the 0-type and the 4-type. The X-type represents a mixture of small and large pustules, for example, of the 1-type and the 4-type. It occurs rather commonly on durum wheat varieties when inoculated with certain races of wheat stem rust.

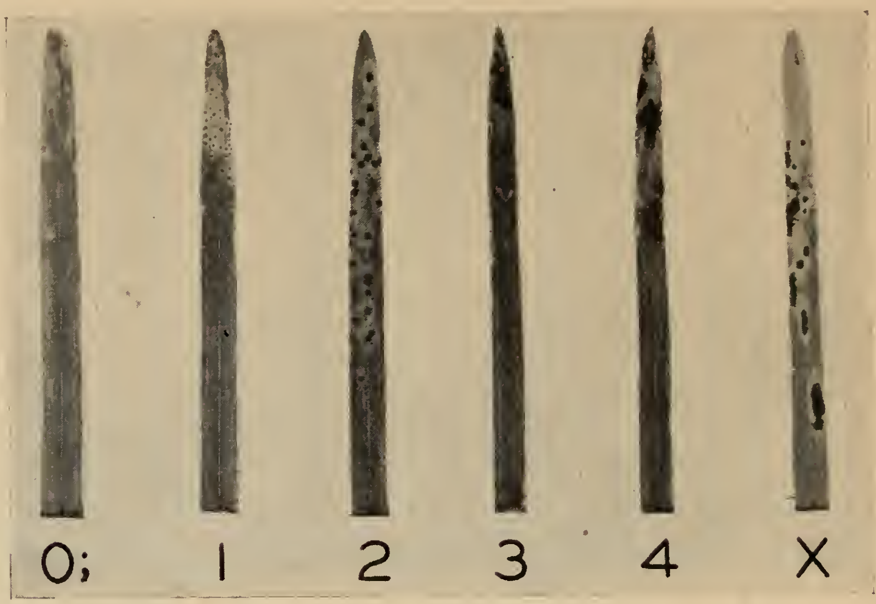

Figure 17.—Types of infection and the symbols by which they are represented. The type on the left (0;) indicates very high resistance. The next four types (1, 2, 3, and 4) indicate increasing susceptibility. The type on the right (X) indicates an indeterminate reaction, but usually more resistance than a 4-type. About natural size. (After Newton and Johnson)

To illustrate how one race differs from another race, there are given in Table 1 the infection types produced on the differential wheat varieties by several of the physiologic races of wheat stem rust that have occurred more or less commonly in Canada during recent years. Variations from the infection types shown in Figure 17 are present in this table. By way of explanation, it may be said that the addition to a given infection type of a plus (+) or of a minus (−) denotes, respectively, a slightly greater or slightly less susceptibility than that represented by the infection type shown in Figure 17. A double plus (++) or a double minus (−−) denotes a slightly greater departure than the

TABLE 1.—The infection types produced on the twelve differential varieties by several races of wheat stem rust commonly occurring in Canada

Physiologic race	Little Club	Marquis	Kanred	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Einkorn	Vernal	Khapli
Race 15	4	4−	4=	3++	4=	4=	4=	3++	3++	3++	4±	1=
" 19	4	2−	0;	3−	4=	4=	4=	3++	3++	3	0;	1=
" 21	4	4	0	3++	4−	4−	4−	4=	3++	1=	0;	1=
" 34	4+	4−	4−	4=	4	4=	4=	4±	3++	1=	0;	1±
" 36	4	4	4−	3++	1=	1=	0;	x	3++	3+	0;	1−
" 38	4	2=	4−	3−	x+	x±	x+	x+	x++	4−	1=	1+
" 49	4	4−	0	4=	1=	1−	0;	x=	3+	1−	0;	1=
" 56	4	3+	3+	3+	1=	1=	1=	3+	3+	1=	1=	1−

single plus or the single minus. A combination of plus and minus (±) denotes that the susceptibility varies slightly, being sometimes greater, sometimes less, than that denoted by the type itself.

From the few examples given in Table 1, it will be seen that at least on one of the differential varieties and generally on two or more of them, the infection types produced by any pair of races are distinctly different. For example, Race 19 can readily be distinguished from Race 21 by the types of infection that they produce on Marquis and Einkorn. Race 49 and Race 56 differ very markedly on Kanred. Similarly, a comparison of any other two races on these twelve differential varieties will show differences in infection type to a greater or less degree.

This fact is made evident by an examination of Figure 18. In this figure, seedling leaves of five of the twelve differential wheat varieties are shown. The upper set of leaves was inoculated with Race 21 and the lower set, with Race 36. It will be seen that the same wheat variety may be very resistant to one race, as Kanred to Race 21, and very susceptible to another race, as Kanred to Race 36. Of course, the difference between one race and another is not always so clearly marked as in this particular case; but, in general, the distinction is pronounced enough to make the separation of one race from another a matter of no doubt. The same is true for races of oat stem rust. Owing to the fact that rye is a cross-fertilized cereal, the varieties in it are usually more or less impure, and on this account the distinction between one race and another of rye stem rust is not generally so clear-cut as in wheat stem rust or oat stem rust.

The existence of physiologic races within the varieties of stem rust largely explains why a variety of wheat may appear resistant to stem rust in some years and be severely attacked by it in other years. If, in any season, only stem-rust races to which the variety is resistant are present in the area where the variety is growing, the variety will be more or less free from rust. If, in another season, races of stem rust to which the variety is susceptible are very prevalent, the variety will become badly rusted. It is clear, therefore, that before a variety, say, of wheat can be declared highly rust-resistant, it should be tested against all races of wheat stem rust, or at least against enough of them to ensure that there is little possibility that any race will do it injury. Similarly, an oat variety should be thoroughly tested against all races of oat stem rust.

For this reason, it is an important phase of rust research to discover what physiologic races of stem rust are present in a country, particularly if an attempt is being made in that country to develop rust-resistant varieties of cereals. This phase of the work must be continued over a period of years, for it is possible, and indeed it happens, that a race not present in one year, or even for several years, may be very prevalent in other years. Occasionally, too, new races are discovered. In order to have races with which to test cereal varieties, it is necessary to keep on hand the races found in the field, or, at any rate, representative races, so that they may be available when needed for use in such tests.

A complicating factor in the identification of physiologic races is the existence of biotypes within certain races. A biotype is a strain of a race; it is distinct from the race in disease-producing ability but cannot be distinguished from the race by the infection types it produces on the regular differential varieties. To distinguish it, another differential variety has to be used. Thus Race 15B cannot be differentiated from Race 15 by the regular differential varieties, but, as Race 15B heavily attacks the variety Lee and Race 15 does not, the two can be distinguished by using Lee as the additional differential variety.

In consequence of the existence of strains within races, the rust investigator has to be on guard against not only new races but also potentially dangerous strains in races already known.

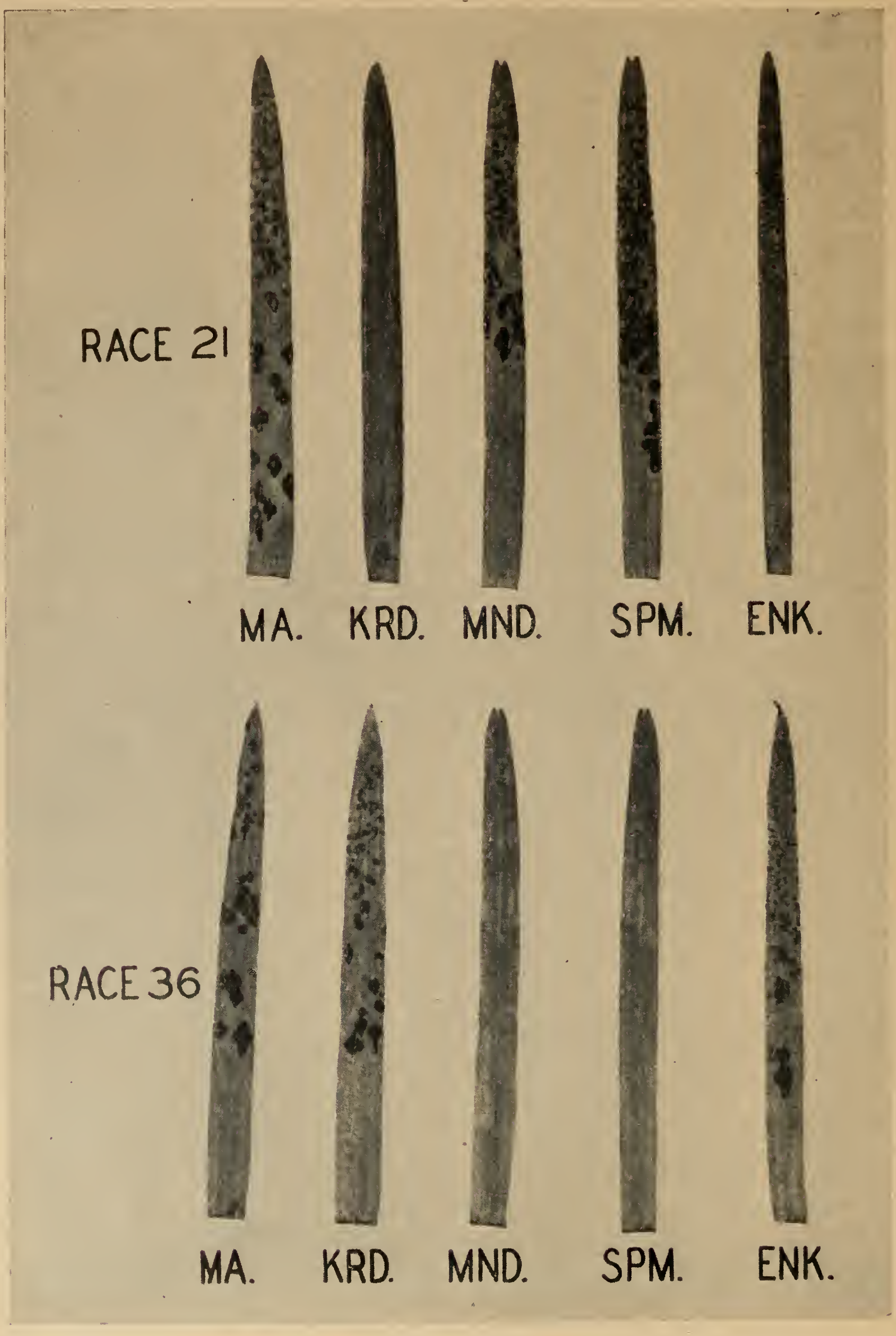

Figure 18.—Infection types produced by two different physiologic races of stem rust on seedling leaves of the same wheat varieties. Notice the contrasting types of infection produced by the two races. (Ma.=Marquis, Krd.=Kanred, Mnd.=Mindum, Spm =Spelmar, and Enk.= Einkorn.) Somewhat enlarged.

HYBRIDIZATION IN STEM RUST

In the account already given of the life cycle of the stem-rust fungus, it was said that when a black spore germinates (Figure 11) each of the two cells of the spore sends out—although not always simultaneously—a stout tubelike process (promycelium) that gives rise to four tiny colorless spores (sporidia) and that the sporidia are able to infect young leaves of barberry. Throughout most of its life cycle the stem-rust fungus has two nuclei (conjugate nuclei) in each cell. For instance, each aeciospore, each red spore (Figure 19), and each cell of the fungus mycelium in the wheat, oat, or rye plant has two nuclei. Before germination, each of the two cells of every black spore also contains two nuclei. When, however, one of these cells begins to germinate, the two nuclei in it fuse together to form one nucleus. This fusion nucleus now divides into two daughter nuclei, and then each daughter divides, so that finally there are four granddaughter nuclei. These pass from the promycelium into the sporidia, one entering each sporidium.

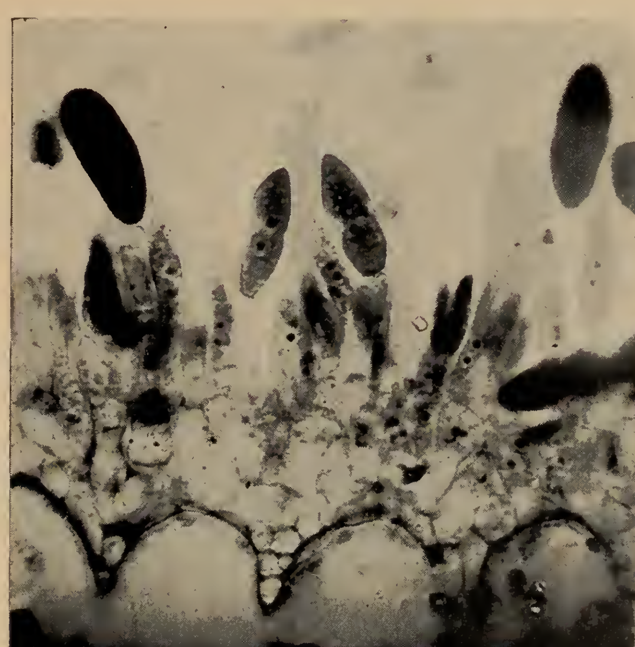

Figure 19.—A section through a young unruptured pustule of stem rust on a wheat stem. Notice the two conjugate nuclei in the immature spores. Magnification, 700. (After Newton and Johnson)

In this process of nuclear fusion and division, there is opportunity for segregation and recombination of character-bearing factors, such as sex factors, to take place. (Other factors also may be reassorted during the process, but the sex factors are the ones of immediate concern here). It has been found that two of the four sporidia are of one sex and two of the opposite sex. As the four sporidia are exactly alike in appearance, the terms "male" and "female" are inappropriate. To indicate, however, that the sporidia differ in their sexual behavior, two of them are said to be of plus (+) sex and the other two, of minus (−) sex.

Now, if one of these sporidia, say, of (+) sex, infects a barberry leaf, it produces a pustule (Figure 20) of the same sex as itself. The vase-shaped structures (pycnia) develop and produce pycniospores and nectar, but no aecia, and consequently no aeciospores are formed. In other words, the pustule

does not fulfil its proper function, namely, to produce aecia and aeciospores. Similarly, if a sporidium of (−) sex infects the leaf, no aecia or aeciospores are produced.

Figure 20.—Underside of a barberry leaf, showing two pustules of stem rust. Each pustule arose from a single sporidium, and is of the same sex as the sporidium from which it originated. Neither has produced aecia. Slightly enlarged. (Photograph by Mr. A. M. Brown)

Figure 21.—A compound pustule of stem rust on a barberry leaf. An infection by a (+) sporidium has fused with an infection by a (−) sporidium, and, as a result, aecia have been produced in the compound pustule thus formed. Magnification, 4 app.

Compound Pustules

If, however, a (+) sporidium and a (−) sporidium infect the barberry leaf so that the two infections are near to each other (a quarter of an inch or less apart), each infection develops into a pustule having pycnia, pycniospores, and nectar. In the course of some days, the two pustules meet and fuse together to form a compound pustule. The mycelium in one portion of the compound pustule thus formed is of (+) sex, and the mycelium in the other portion, of (−) sex. When the fusion occurs, the mycelium of one portion comes into contact with that of the other portion, and, being of different sex, they interact. The interactions consist essentially in an exchange of nuclei, so that the (+) mycelium receives (−) nuclei, and the (−) mycelium (+) nuclei. The binuclear (conjugate) condition is thus re-established, and the mycelium then proceeds to develop aecia and aeciospores (Figure 21).

There is just as good a chance, of course, that two sporidia of the same sex may cause two infections near together on a barberry leaf as there is of two sporidia of opposite sex doing so. If the two sporidia are of the same sex, both (+) or both (−), the two pustules arising from the infections may meet and fuse, but no aecia develop. In other words, such a compound pustule behaves like a pustule that originates from a single sporidium.

The chances of compound pustules being formed depend very largely on how numerous the infections are. If they are many, there is a better chance of compound pustules being formed than if they are few and scattered. In any case, only about half the compound pustules develop aecia, for only about half of them have one portion of (+) sex and the other portion of (−) sex. In fact, if the fungus did not have another method by which it could induce aecia to develop, it would probably not be so successful in continuing its existence.

Action of Pycniospores

In this second method, it is not necessary that pustules of opposite sex develop close together: contact between such pustules is established in a totally different way. Owing to the fact that the nectar produced by the pycnia is sweetish and that the upper surface of the pustules is of a rather bright orange color, flies and other insects are attracted to the pustules. As they go from pustule to pustule, sipping the nectar, they carry pycniospores from one pustule to another. As a result of this intermixing, pustules of (+) sex receive pycniospores of (−) sex, and pustules of (−) sex receive pycniospores of (+) sex. The fungus threads (hyphae), referred to earlier, that protrude through the openings of the pycnia (Figure 22) come into contact with the pycniospores of opposite sex, brought by the insects, and an interaction takes place between the pycniospores and the threads or hyphae. Nuclei of the pycniospores pass over into the hyphae and thus re-establish the binuclear (conjugate) condition in the mycelia of the pustules. Something akin happens as takes place when a flower is fertilized by pollen.

When insects are plentiful and active, as they usually are, this is a more effective method than the other one for re-establishing the binuclear condition, for by it most of the pustules develop aecia and aeciospores. This method of inducing single pustules to form aecia has been found very convenient in experimental work. The nectar can be transferred from pustule to pustule by hand, with the aid of a toothpick, knife blade, or other implement, just as effectively as insects can transfer it. Figure 23 shows how effectively the transfer can be done by hand. The nectar of all the infections on the right of the midrib was intermixed, receiving composite nectar collected from other infections, and practically all of the infections developed aecia; the nectar of the infections on the left of the midrib was not intermixed, and none of the infections developed aecia.

Figure 22.—A thick cross-section through a stem-rust pustule on a barberry leaf, showing a side view of a pycnium. Notice the two types of hyphae emerging through the opening at the top of the pycnium. Magnification, 400 app.

Figure 23.—The under side of a barberry leaf showing a number of infections without aecia on the left of the midrib, and a number with aecia on the right of the midrib. Composite nectar (collected from many other infections) was applied to the upper surfaces of the infections on the right. The infections on the left received no nectar from any other infection. Through the action of the pycniospores in the composite nectar, the pustules on the right were induced to develop aecia. Magnification, 2 app.

Crossing of Races and Varieties

Because the stem-rust fungus passes through this sexual phase of its life cycle on barberry, the opportunity therefore exists in this phase for crossing to take place between physiologic races of the rust. Suppose a barberry bush is growing in the vicinity of a wheat field in which, say, Race 21 and Race 36 of wheat stem rust are present on the crop. These races, in the black-spore stage, will survive the winter on straw and stubble. In the spring the black spores will germinate, and sporidia of both races will infect the barberry leaves. Some pustules of Race 21 will likely arise near pustules of Race 36. Wherever a (+) pustule of Race 21 and a (−) pustule of Race 36, or a (−) pustule of Race 21 and a (+) pustule of Race 36, are near enough together to fuse, the compound pustule so formed will give rise to hybrid aeciospores.

Many of the pustules, of course, will be too far separated for fusions to occur, but flies and other insects visiting such pustules will intermix the pycniospores, so that pycniospores from pustules of one race will be transferred to pustules of the other race, and as a result hybridization between the two races will occur, and hybrid aeciospores will be produced in these pustules also. There is good evidence that crossing between different physiologic races of stem rust actually takes place.

Under greenhouse conditions, numerous crosses have been made between races of wheat stem rust by transferring by hand the pycniospores of pustules of one race to pustules of another race. From such crosses, upwards of 50 different physiologic races of wheat stem rust have been produced. Most of these races have never been found on crops in the open field. None of these new races, however, attacks wheat more severely than do some of those races that occur commonly outside in nature. This is not to say, however, that a race worse than any now known may not arise through hybridization.

Crosses have also been made between different varieties of stem rust, such as between wheat stem rust and oat stem rust, or between wheat stem rust and rye stem rust, and true hybrid races have been procured. There is, however, considerable intersterility between such varieties of stem rust, while within any variety the races appear to be completely interfertile, so that hybrids between any two races, say, of wheat stem rust can readily be obtained.

SOURCES OF INFECTION

Of the five spore types of the stem-rust fungus, only two, the cluster-cup spores (aeciospores) and the red spores (urediospores), can infect cereals and grasses. If, therefore, an outbreak of stem rust occurs in any particular region or area, it must first have originated either from infected barberry or from the red stage that has survived from the previous year. Within some particular region, of course, it may happen that neither source is present, the outbreak being started by wind-borne spores that originated elsewhere.

Infected Barberry

For barberry to be a source of infection, stubble or straw of grain or grasses bearing black spores must be present in the vicinity of barberry so that, when the black spores germinate, the sporidia formed can reach it and infect it before they dry up and die. Weather conditions that are such as to permit free germination of the black spores are usually favorable for abundant infection of barberry.

In order, however, that the disease may spread from barberry, it is not necessary that grain crops be growing in the immediate neighborhood of an infected bush, although the nearer they are, the greater is the chance for heavy

infection to occur. Aeciospores, although perhaps not so resistant as urediospores to heat and dryness, may be carried considerable distances and still be able to cause infections. Moreover, grasses growing in the vicinity of an infected bush may become heavily infected, and urediospores produced on them may then spread to cereal crops.

Survival of Red Stage

When the source of infection is the red stage that has survived from the previous year, the early infections are caused by urediospores, instead of by aeciospores. The period between two crop seasons corresponds, in cooler climates, to the winter months, and, in warmer climates (where winter crops are grown), to the summer months. Generally speaking, this period is considerably longer than the period that urediospores can remain alive under ordinary outside conditions. Usually they either germinate when there are no green plants present to infect, or they perish without germinating. In both cases, the end result is the same.

It is true that, under certain constant conditions of temperature and air humidity (about 40° F. and 50 per cent relative humidity), urediospores may remain living for upwards of nine months or even for a year, but such conditions rarely occur in nature. The possibility, however, of their living long enough to infect the next year's crop cannot be altogether excluded; but wherever the red stage is known definitely to survive from one crop to the following one, it does so apparently on susceptible grains or grasses that remain green during at least most of the intervening period. The fungus continues to grow and feed, although perhaps at a much reduced rate, during the whole or the greater part of the period between crop seasons.

Whether infection in an area arises from the one or the other source, or from both sources, depends very largely on the climate of the area concerned, and, of course, on whether or not barberry is present. If barberry is not present, it cannot be a source of infection. Generally speaking, the red stage persists from one season to the next only in areas or countries having a mild climate. For instance, in Europe, the chief source of infection is the barberry, for the red stage of stem rust seems to be quite generally killed out during the winters, although in Southern Europe it appears that this stage may overwinter to some extent in very mild winters. The opposite situation exists in Australia. There the source of infection is the red stage. This stage, owing to the mildness of the climate, survives from one crop season to another on self-sown, or volunteer grains. Barberry has been introduced only to a limited extent, and it plays little or no part as a source of infection.

Sources in North America

In North America, climatic conditions vary from cool temperate in the northern agricultural zone to subtropical or even tropical in the southern zone. Therefore on this continent both sources of stem rust are present: infected barberry in the cooler parts and the overwintered red stage in the warmer parts. Barberry rusts quite generally in Canada and in the northern United States. A native species rusts farther south in some of the mountain districts in the eastern part of the United States. Native species occur in the southern Great Plains region and in the Rocky Mountains but they rarely become infected.

There is one important cereal-growing region in which barberry is present but seldom becomes infected with stem rust. This is the southern half of the Mississippi Valley. In this region cereal crops ripen in early summer, and the black spores, formed at that time, are therefore exposed to the intense midsummer heat, which kills them. Consequently, they do not germinate in the following spring, and so barberry very generally escapes infection.

Of the stem rusts that attack cereals, the only red stage known definitely to overwinter in Canada or the northern United States is the variety on rye. It is able to survive the winter on heavily infected couch grass as far north as Winnipeg. The variety of the rust that attacks timothy can survive the winter in the northern United States and adjacent parts of Canada, and the varieties that attack red top and blue grass may be capable of similar survival. The overwintering of wheat stem rust and oat stem rust seems to be confined to Mexico, the American states bordering on the Gulf of Mexico, and the Pacific coastal region, particularly southern California.

INFLUENCE OF WEATHER

Stem rust cannot increase rapidly or spread widely unless climatic or weather conditions are favorable for its development. Generally speaking, weather conditions that are favorable for rapid growth of crops are also favorable for the development of the disease. Certain other factors besides weather conditions influence the rapidity with which the disease develops and spreads, but these other factors would be largely inoperative in the absence of weather conditions that favor the development and spread of the disease. A combination of favoring conditions would allow the disease to make greatest progress. The principal climatic factors influencing the development of stem rust are moisture, temperature, and wind or air currents.

Moisture

A film of moisture must be present on the plants before the spores will germinate, and it must remain long enough to allow the germ tubes to enter the breathing pores of the plants. A few infections may occur within four or five hours, but for abundant infection the plants must remain damp for upwards of 24 hours. If the plants become dry before the germ tubes enter them, the germ tubes wither and die. This is one of the reasons why thin crops, which dry quickly after a rain or dew, are usually less heavily rusted than thick rank crops, which dry much less rapidly. However, once the fungus gains entrance into the plants, it is no longer dependent on outside moisture. It is then able to make use of the moisture in the plants themselves.

Temperature

Certain limitations on the development of the disease are imposed by temperature. Little infection can occur below 50° F. or above 90° F., and growth of the fungus inside the plants ceases at about these limits. Infection proceeds most freely and growth most rapidly between 65° and 75° F. There is a marked slowing down of growth when the temperature falls below 60° or rises above 85° F.

Wind

Stem rust cannot spread unless spores of the fungus are distributed, and wind is the greatest distributing agent. Usually there is sufficient wind during the growing season to carry the spores from plant to plant, from field to field and for long distances. Spores have been thus carried for upwards of a thousand miles. Strong winds passing over a large rust-infected area pick up and carry along enormous numbers of spores, thus causing at rather distant points the so-called "spore showers". Such showers, in Western Canada, occur after a day or two of strong south wind.

Severe outbreaks of stem rust usually occur in seasons when moisture is plentiful and the average temperature is above 62° or 63° F. Damp misty days alternating with bright warm ones, or dewy nights followed by warm

sunny days favor infection and growth of the fungus in the plant tissues. Continued cool weather retards the development of the disease; but if during a period of cool weather rains or dews occur, many infections may take place, and if the weather then turns warm, the heat hastens the development of the fungus in the plants, and within a few days there may be a sudden increase in the amount of rust. Dry cool weather gives a susceptible crop the best protection against stem rust. Dry hot weather has a similar influence, but it tends to induce premature ripening and hence prevents proper filling of the grain. During the summer, dry hot weather occurs more commonly than dry cool weather. Not infrequently in the Prairie Provinces, the grain crop has been saved from extreme stem-rust damage by a spell of very hot dry weather that checked the disease and hastened the maturing of the crop.

RELATION OF SPORE ABUNDANCE TO EPIDEMICS

The rapidity with which an epidemic of stem rust can sweep over a whole countryside for hundreds of miles, and even for greater distances, has always been, and is yet, an amazing phenomenon. It is little wonder that in earlier times, and not so far back even in modern times, a severe outbreak of stem rust was regarded as a visitation of Divine displeasure. How else, it was imagined, could destruction be so swift and sure? Like so many other mysteries, this one, too, has been solved by careful and prolonged investigation.

An epidemic of the disease is the result of countless numbers of infections. In order, therefore, that an epidemic may develop, an enormous number of spores must be produced. Each pustule of stem rust arises from an infection by at least one spore. Under epidemic conditions, plants may be almost completely covered with pustules. The fact that millions and millions of acres may be, and often are, thus affected, indicates how very great must be the number of spores necessary to produce such a condition.

Not all the spores, by any means, succeed in causing infections. As they are distributed by wind, great numbers of them fall to the ground, or lodge on nonsusceptible crops, or are blown away to forest, lake, or ocean. The wastage of spores is, therefore, very great, and hence the ones that chance to lodge on susceptible crops make up only a part, perhaps only a small part, of the total number produced.

Factors Influencing Spore Abundance

The production of such a vast number of spores requires time. The length of time, of course, depends on the rapidity with which spore multiplication goes on. If the rate of multiplication is too slow, no epidemic can develop. Weather conditions, as already indicated, have a pronounced influence on the rate of multiplication; but, in addition to the weather, certain other factors play a part.

One of these factors is the number of spores that spreads from the source. This number, in turn, depends on the number of barberry bushes present and the extent to which they are infected or on the amount of overwintering that has occurred. Another factor is the earliness with which spores spread from the source. In ordinary summer weather, an infection by an aeciospore or a urediospore takes approximately one week to produce a new generation of spores. It is obvious that, other things being equal, the earlier that spores begin to spread from the source, the greater is the number of spore generations that can be produced in a season. Then, again, as it is a matter of chance where the spores fall, it can readily be seen that the more extensively susceptible cereal crops are grown the better are the chances of the spores lodging on plants that they can infect.

CHARACTERISTICS OF SPREAD

Within Region of Source

The first stage in the spread of the disease occurs in the region where the rust has its source. This region may be large or small. In Australia, for example, it is large, for overwintering—actually "oversummering"—occurs to a greater or less extent throughout the cereal-growing area. On the other hand, in India, it is small in comparison with the area subsequently affected, for it seems to be confined to restricted areas in the foothills of the Himalaya Mountains, from which locality the disease spreads to the plains. In North America the area where barberry becomes rusted is large, while that where overwintering occurs is relatively small.

When spores begin to spread from an infected barberry or from a point where the rust overwintered, more spores lodge in the immediate vicinity of the barberry or the overwintering spot than at points farther distant. There is a tendency, therefore, for infections to be most numerous around such centers of infection and to diminish with increasing distance from them. For this reason, the early stages of stem-rust spread are characterized by the occurrence of comparatively small, more or less isolated rusted areas, the number of which depends on the number of locations with infected barberry or the number of points where the rust overwintered. At first, only a few infections may be present in each center, but, as aeciospores or urediospores continue to be liberated, and as each new infection gives rise to a new generation of spores, the severity of the infection in each of the centers increases and the area involved becomes larger. In the course of a few weeks, these localized outbreaks may produce sufficient spores to cause a general infection of the whole region, and eventually perhaps give rise to epidemic conditions.

Beyond Region of Source

While stem rust is increasing in the barberry or overwintering region, the crops in that region are steadily progressing towards maturity, and when they ripen no further increase of spores can take place. In the meantime, however, spores are blown away by the wind in different directions. Some of these spores may be carried to a neighboring area where no source of infection is present. At first only relatively few spores may arrive, but as the disease makes headway in the region of the source, the number of spores arriving in the neighboring area increases. Distinct spore showers may occur when the wind blows from the direction of the former region. If green susceptible crops are present and weather conditions are favorable for stem-rust development, infections occur, at first only a few, but later in greater numbers. In contrast, however, to the early stages of spread in the region of the source, the infections are usually more or less uniformly distributed, as would be expected of infections arising from spores carried relatively far by winds.

In the course of a few weeks, stem rust runs its course in this second area, but during that time spores produced on crops growing in it are blown away to other areas. If in any of these areas there are green susceptible crops, the disease may become established in them, and with favorable weather may cause serious loss. Therefore, as long as there are green susceptible crops to infect and weather conditions favorable for infection, an outbreak of stem rust may advance a very long way from its source.

As crops ripen successively later from the equator northward or southward, it would be expected that the usual direction of spread in the northern hemisphere would be from south to north, and, in the southern hemisphere, from north to south. This is, as a matter of fact, the general direction of spread. For instance

in Eastern Asia, stem rust spreads northward from Manchuria into the Amur region. In some years at least, stem rust seems to spread from Asia Minor to the Balkan Peninsula and northward through Central Europe. Some of the infection comes from infected barberry, so that the northward spread is not always very clearly defined. In India, however, the direction of spread is reversed, for stem rust spreads from the foothills (of higher elevation) in the north to the plains (of lower elevation) lying to the south. In the southern hemisphere, stem rust spreads from southern Brazil, where it overwinters southward to Uruguay and Argentina. In Australia, the disease first becomes prevalent in the more northerly cereal-growing areas, and spores originating there are blown southward and intensify the attack in the more southerly areas where, in any case, some infection from the overwintered red stage would occur. Southward-blown spores appear responsible for outbreaks of stem rust in the Cape province in the Union of South Africa.

STEM RUST SPREAD IN NORTH AMERICA

To illustrate some of the observations made above, consideration may be given to the spread of stem rust in North America. As cereal production is carried on much more extensively in the Mississippi Valley in the United States and in the Prairie Provinces of Canada than elsewhere on this continent, and, as these two areas have suffered greater damage from the disease than have any other areas, attention may first be given to them.

Mississippi Valley and Prairie Provinces

As far as the spread of stem rust is concerned, these two areas must be regarded as one. They embrace an almost continuous cereal-growing belt, extending from the Gulf of Mexico to the Peace River Valley in northern Alberta. From south to north, crops mature successively later, so that, when those in the extreme south are ready to harvest, those in the extreme north are being seeded or are just beginning to show above ground. In these two respects, therefore, this extensive cereal-producing belt is well adapted to the long-distance spread of the disease. Furthermore, since an overwintering region for stem rust comprises the southernmost portion of this belt, namely, central and southern Texas, with suitable weather conditions during the course of the spring and summer, an outbreak of the disease originating in the overwintering area might spread throughout the whole length of the Mississippi Valley and on into Canada as far north as cereal crops are grown.

Only in some years, however, is there very clear evidence of such a northward spread from the overwintering region of the rust in the south. As a matter of fact, the southern half of the Mississippi Valley has been less subject than the northern half to outbreaks of stem rust. One of the principal reasons for this is that, in the northern half, the disease spreads from infected barberry. Outbreaks originating from this source, particularly those in the Upper Mississippi Valley, spread on northward into the Prairie Provinces. Undoubtedly the eradication of barberry, which has been in progress in the northern half of the Mississippi Valley for 35 years or more, has reduced very appreciably the importance of barberry as a source of infection in this region. By reducing the number of barberry bushes, the number of centers from which infection can spread is reduced, and as a result there is less opportunity of a general infection developing, with the consequent possibility of its attaining epidemic proportions.

The northern half of the Mississippi Valley is exposed to invasions of stem rust from the south, and also to attacks arising locally from barberry. In some years, therefore, infections arise both from northward-blown spores and from locally-produced spores. If stem rust becomes prevalent and severe in

this area, more especially in the Upper Mississippi Valley, the chances of the Prairie Provinces escaping a serious attack are very slight indeed. As a matter of fact, when stem rust is heavy in the Upper Mississippi Valley, it is usually heavy in the Prairie Provinces, at least in Manitoba and eastern Saskatchewan, and, when stem rust is light in the former region, it is usually light in the latter. Whether an outbreak of stem rust in the Prairie Provinces originates in the extreme south (in the overwintering region) or in the northern part of the Mississippi Valley, it always comes as a northward advance of the disease from the Upper Mississippi Valley.

In the Prairie Provinces, infections almost invariably appear first in Manitoba, then in Saskatchewan, and last in Alberta, usually a month or more later than in Manitoba. In each province, wind-borne spores are usually present one or two weeks, sometimes longer, before the first infections appear. Spores are always more numerous in Manitoba than in Saskatchewan, and in Saskatchewan than in Alberta. Western Saskatchewan and certainly Alberta seem to lie to the west of the main northward drift of spores, whereas Manitoba, especially in Red River Valley, and eastern Saskatchewan to a lesser extent are apparently directly in it. Hence, outbreaks in Manitoba particularly, and in eastern Saskatchewan, occur much more often and in much greater severity than in western Saskatchewan and Alberta. Spread toward the west, of course, takes place but it is usually more gradual than to the north, so that by the time the disease gets fairly well established in Alberta, the bulk of the crop in that province is mature. To a lesser extent, the same is true of western Saskatchewan.

There is one aspect of the spread of stem rust in the Mississippi Valley and the Prairie Provinces that has not yet been referred to and about which there is still some uncertainty. As already mentioned, cereal crops in Texas ripen in late spring. The summers there are intensely hot, and conditions in the cereal-producing area are such that stem rust would have great difficulty in persisting through the summer. Cereals, except perhaps occasional volunteer plants in protected situations, are absent, and grasses are largely withered by the heat. The red stage, therefore, rarely persists through the summer. The black spores are killed by the heat, and barberry thus escapes infection. Notwithstanding these conditions, infections appear in autumn and early winter on fall-sown grain.

There is little chance that the spores responsible for these infections come from northern Mexico, unless the red stage of the rust can oversummer on some of the higher plateaux. Though there is evidently some survival of rust during the summer in Texas, Oklahoma, and other southern states, the probability is that the spores come principally from those northern areas in which stem rust builds up to enormous quantities during the summer. When there is a late harvest in the Dakotas and the Prairie Provinces, as happened, for instance, each year from 1950 to 1954, there is unquestionably a southward movement of rust spores, some of which cause infection on fall-sown wheat in Texas and adjacent states. Thus, there is not only a northward movement of the rust in early summer but also a southward movement in autumn. This movement and countermovement of the rust probably provides the reason for the persistence, year after year, of certain rust races, once they have become established in the Mississippi Valley area.

Remainder of Continent

Although stem rust is of less importance in other parts of the continent than in the Mississippi Valley and the Prairie Provinces, it is, nevertheless, responsible for considerable damage elsewhere. In the semiarid Great Plains area, which lies west of the Mississippi Valley, stem rust is not usually of much importance, but occasionally, as in 1904 and 1935, a heavy infestation occurs.

In the southern part of this area, native species of barberry seldom become infected and hence play little or no part in the spread of the disease. It would appear that when outbreaks occur in this area, they are largely attributable to spores blown in from the Mississippi Valley. The northern part lies in the barberry-eradication area of the North-Central States, and where barberry occurs there is the possibility of infection spreading from this source. Undoubtedly wind-borne spores from the south and east influence the amount of infection in this part.

West of the Great Plains area of the United States and the Prairie Provinces of Canada, the area suitable for cereal production is comparatively small and much divided owing to the mountainous nature of the country. Overwintering occurs in the Pacific coastal region, where outbreaks of the disease are usually severe and of rather frequent occurrence. In some of the mountain valleys, stem rust apparently overwinters occasionally, and there is the possibility, as happened in 1904, of spores being carried in from the Mississippi Valley and the Great Plains by wind. The Inland Empire, between the Rocky and the Cascade Mountains, is an important agricultural area, but there stem rust does not appear to overwinter. In some of the grain-growing areas barberry was of considerable importance as a source of stem-rust infection before eradication was undertaken in 1944.

Farther north, in British Columbia, grain-growing is of minor importance, and the occurrence of stem rust there has not been given much attention. Barberry hedges are rather common in the lower Fraser River Valley, and infection from them causes considerable damage to oats, the principal cereal crop. In the interior valleys, barberry seems to be very scarce, and stem rust is seldom of any consequence. A native species occurs, but it rarely rusts. The possibility of stem rust overwintering has not been investigated, and nothing is known concerning the importance of wind-borne spores.

In Mexico, stem rust persists throughout the year in certain areas such as the southern plateau and parts of the west coast; but rust spores are probably not blown in significant numbers from these far-away regions to Texas. It seems likely that the red stage that overwinters in Texas and adjacent northeastern Mexico is the chief source of rust infection for the Mississippi Valley region.

In eastern North America, little attempt has been made to eradicate barberry, and as overwintering of the red stage of stem rust is not known to occur, it is probable that localized outbreaks originate largely or entirely from infected barberry. Undoubtedly much of the infection in the Eastern States arises from this source. Localized outbreaks, for instance in the Allegheny Mountain region, have been repeatedly traced to barberry. There seems, however, to be no good reason why wind-borne spores from the Mississippi Valley may not be responsible for considerable infection in these states. In most years, however, it appears that localized outbreaks occur rather than general infections. Stem rust is present every year in Eastern Canada, and surveys, particularly in Ontario, have demonstrated the occasional relation of barberry to local outbreaks of rust. There is not much probability that overwintering occurs to any considerable extent.

In some years, however, the distribution of the disease in Eastern Canada seems to be much too general and uniform to be accounted for satisfactorily by spread from local sources. It would appear that these general outbreaks are attributable to invasions of wind-borne spores from states lying to the south and southwest. As a matter of fact, there seems to be a relationship between the occurrence of stem-rust epidemics in the Mississippi Valley and heavy general infections in Ontario—certainly in western Ontario—and possibly in Quebec. Not enough is known about general outbreaks in the Maritime

Provinces to relate such outbreaks to epidemics in the Mississippi Valley or Eastern States but it seems probable that these provinces are well within the range of wind-blown spores from areas south and east of the Great Lakes.

Figure 24.—Seed of Marquis wheat grown in 1935. Left.—Seed from plants badly damaged by stem rust. Right—Seed from plants uninjured by stem rust. About natural size. (Photograph by Mr. A. M. Brown)

EFFECT OF STEM RUST ON CEREAL PLANTS

A heavily rusted crop produces shriveled light-weight seed (Figure 24), so that the yield is much reduced and the quality and grade of the grain are lowered. How are these results brought about? It must be remembered that the fungus causing stem rust is a parasite which infects green growing plants. In order to develop, it must obtain its food and water from the plants that it attacks. In cereal plants, therefore, the fungus uses the food that would otherwise be carried up to the heads to fill the kernels. Besides, as the fungus develops that is to say as the mycelium in the infections grows, it produces numerous pustules, and these, breaking out, do great injury to the surface of the plants. As the manufacture of plant food takes place largely in the cells at or near the surface, this process is very seriously interfered with in rusted plants. In these two ways, therefore, the fungus reduces the food supply within the plants. It also reduces the water supply within the plants. It needs water as well as food. The water, therefore, that is used by the fungus is lost to the plants. There is a further loss of water, by evaporation, through the numerous ruptures caused by the pustules.

The kernels are, therefore, poorly supplied with food and water and as a result they shrivel. Chemical analyses have shown that badly rusted straw has a higher food value for stock than has unrusted straw. Of course, the higher food value of the rusted straw may be due, in part at least, to the food contained in the fungus within the straw, rather than to the food in the straw itself; but very probably some of the food that should have reached the kernels is left in the straw because of insufficient water to carry it to the heads.

The belief has been rather commonly held that the fungus living in the stems of the plants is able to draw away from the kernels food that had already been stored in them. Grain was frequently cut "on the green side" to prevent

this withdrawal of food. There is no good evidence for this belief. Careful experiments by different investigators at different times and in different places go to show that rusted grain yields best when it is cut in the hard dough stage that is, when the kernel cannot be readily crushed by pressure between the thumb and forefinger. At this stage there may be less water in the kernels than there was earlier, and on this account the kernels may look less plump, but the actual weight per bushel of dry threshed grain is greater. It is not advisable, however, to allow a rusted crop to stand until it is dead ripe. The straw becomes brittle, and harvesting is difficult. Moreover, many heads may break off from the brittle straw and thereby reduce the yield.

Figure 25.—Comparison of seedlings grown from seed of badly rusted and of unrusted wheat. Left.—Seedlings from seed badly shriveled by stem rust ('Feed' grade). Right.—Seedlings from seed uninjured by stem rust (No. 1 Northern). Notice the slender delicate plants on the left in contrast to the vigorous strong ones on the right. (Photograph by Mr. A. M. Brown)

Another belief was that if a rusted crop is cut green, considerable filling of the kernels takes place after the crop is cut. Experiments, however, have shown that this belief is not well founded. The movement of food from the straw into the kernels ceases soon after the crop is cut, so that little or no filling can take place.

It has been known for many years that badly shriveled kernels make poor seed grain. The germination of such kernels may be good, but the seedlings produced by them are generally weak (Figure 25). These seedlings suffer from partial starvation, as the kernels have an insufficient amount of food stored in them to support vigorous seedling growth until the young plants can get established and begin to manufacture food for themselves. If such seed is sown rather deeply, the seedlings have difficulty in emerging and becoming self-supporting. Moreover, in recent years, it has been found that weak seedlings are much more likely than vigorous ones to be injured by root-rotting fungi living in the soil. The effect of stem rust, therefore, finds expression not only in the crop that is attacked but also in the crop arising from the seed of the crop that it has injured.

CONTROL OF STEM RUST

Stem rust is a difficult disease to control. It is widely distributed throughout the world, it is spread by wind, it increases very rapidly, and the crops that it attacks are very extensively grown. It is not seed-borne, although, when a

crop is heavily rusted, kernels may become infected while still immature. When seed thus affected is sown, it does not produce rusted plants. Seed treatments, such as are used for the control of cereal smuts, are therefore of no value in controlling stem rust. Infections only arise from spores that come into contact with the above-ground parts of the plant. Owing to the extensive scale on which cereals are grown, control measures must be practicable for relatively large areas if rust losses are to be measurably reduced. Of course, the protection of a single farm or field would be of decided benefit to its owner; but the problem of stem-rust control must be regarded largely in its broader aspect. The more permanent and widely effective the method, the more valuable must it be considered.

Destruction of Barberry

It has been pointed out that infected barberry may serve as a source of infection. In some areas it is the chief or only source. Furthermore, races of stem rust may hybridize on it and produce new races. On both counts, therefore, it is a menace to cereal crops. Wherever in a cereal-growing area it is known to rust, it should be destroyed. In so far as it is the source of infection, its destruction is a permanent and widely effective means of control.

Early Maturity

Crops that mature early are, as a rule, considerably less damaged by stem rust than are those that mature later. One reason for this is that the amount of infection almost invariably increases as the season advances. Another reason is that by the time the disease becomes very prevalent and severe, the early crop is more fully developed than the later one. That is, more food has been stored in the kernels of the early crop. The less mature a crop is when the disease becomes severe on it, the less chance have the kernels of filling well. A difference in maturity of one week often makes a pronounced difference in the amount of injury. Early maturity does not confer resistance on a crop; it only gives the crop a chance to escape damage.

Early maturity can be secured by sowing early varieties. Reward wheat, for example, usually suffers considerably less damage than Marquis from stem-rust, largely on account of its earliness, although actually it is not quite so susceptible as Marquis. Garnet is an early but very susceptible variety of wheat. In heavy-rust years, occasional fields of this variety have been known to escape appreciable damage owing to the fact that they ripened before the disease got well under way. Early seeding brings about the same result. The crop is pretty well along to maturity before the disease becomes severe. Then, again, the addition of phosphate and potash fertilizers to the soil tends to induce early maturity. There are, of course, obvious limitations to the extent of control that can be obtained by early maturity.

Chemicals

To be satisfactory a chemical must be effective in itself and, in addition, it must be available in adequate amounts, methods of application must be practical, and the cost must be commensurate with crop returns. At present no chemical satisfies all requirements.

Zinc ethylene bis-dithiocarbamate (sold under trade names such as Zineb, Parzate, and Dithane Z-78) and sulphur will control rust if several applications are made. These fungicides are toxic to germinating rust spores and prevent the entry of the rust into the plant so long as they are present on the leaf or stem surface in sufficient concentration. They do not destroy the rust after it

has entered the plant. As they can be washed off the plant surface by heavy rains, their effectiveness depends a good deal on the weather immediately following application.

Since 1950, there has been considerable search for a systemic fungicide, a chemical that would be absorbed into the plant and would then be sufficiently antagonistic to the rust to prevent further infection for a period of several weeks. No satisfactory chemical of this type has been found thus far. In some experiments, though not in all, calcium sulfamate has given fair control of rust. This chemical, however, has a tendency to reduce severely the germination of the seed produced by treated plants, and according to some reports it reduces the quality of the grain. For these reasons, calcium sulfamate cannot be recommended; moreover, it is not yet on the market in quantity.

If producers of a chemical to be used could be assured of a constant market, it would be profitable for them to maintain supplies to meet the demand. Rust, however, does not strike every year, and when it does strike, the period during which control measures can be effective is short—at most only a month or six weeks. It might be difficult therefore to provide adequate supplies of the chemical, particularly if the demand were great.

Finding a suitable method of applying a chemical is another problem. Few farmers have the machinery necessary for the application, in dust form, of fungicides such as sulphur or zinc ethylene bis-dithiocarbamate. The latter chemical, however, is available in liquid form and will give control of rust equal to that of sulphur, at a lower cost, if applied in the form of spray. The purchase of machinery is an additional expense and, moreover, the use of ground machinery damages standing grain. Application by airplane might solve this problem but is likely to be expensive, especially in the case of substances such as sulphur, which have to be used in high dosage, a requirement that would involve frequent landings and reloadings. The ideal chemical for airplane application would be one in liquid form that could be applied in low dosages and that would require only a single application for control. No such chemical is yet available.

The final and most important consideration in control of rust by chemicals is the cost. Costs must be relatively low if this means is to be feasible. Sulphur, for example, would probably require three applications of about 40 pounds each per acre to give even moderate control of rust. The total cost is likely to be from 8 to 10 dollars per acre, varying with the year and the locality. If dithiocarbamates were used, as sprays, the cost of materials would be considerably lower.

At present, chemical control, though not impossible, is expensive and uncertain and cannot be adopted over areas involving many millions of acres. However, more effective chemicals at reduced cost are being sought and the situation may improve within a relatively short time.

Plant Breeding

The simplest and best method of controlling stem rust is to grow resistant varieties. A variety, however, may be resistant to stem rust but wholly undesirable in other respects. As a rule, high resistance to stem rust occurs naturally in varieties that are of little or no commercial value. To obtain a satisfactory resistant variety, it is necessary, by plant-breeding methods, to combine high rust resistance and desirable agronomic and commercial characters in the same variety. Even in the simplest case, this may be much more difficult to accomplish than might be expected.

In securing such a combination of characters, the plant breeder meets with two sources of difficulty, one relating to the cereals and one to the fungus. With the cereals, the chief difficulty lies in the fact that a large number of

desirable characters is required in addition to high resistance. For instance, a suitable bread wheat variety must be satisfactory in agronomic characters, such as earliness, strength of straw, yield, weight per bushel, kernel color and shape, and in milling and baking characters, such as flour yield, flour color, gluten quantity, gluten quality, loaf volume and crumb texture. Besides, it must not be unduly susceptible to leaf rust, loose smut, bunt, rootrot, and other diseases. Unfortunately resistance to stem rust is frequently associated with some undesirable character, so that rust resistance and the undesirable character tend to be inherited together, as if they constituted a single character.

With the fungus, the chief difficulty lies in the fact that there are different races or strains of stem rust. A variety of wheat, for example, may be highly resistant to certain races of wheat stem rust, but completely susceptible to other races. A second variety may be highly resistant to some of the races to which the first variety is susceptible. A third variety may be resistant to still other races. If no variety can be found that is resistant to all races, the resistance of two or more of such partially-resistant varieties must be combined. If, on the other hand, a variety can be found that possesses high resistance to all races, and if that resistance is rather simply inherited so that it can be completely transferred to another variety, the breeding problem would be simplified. In this case, the building up of resistance would not be necessary, and hence fewer crosses would be required to accomplish the same result. Care would have to be taken, however, in both cases to get rid of any undesirable character that may be associated with rust resistance.

Success in producing rust-resistant varieties of wheat has been achieved by combining the resistance of two or more varieties in a new variety. For example, Thatcher, originated at the University of Minnesota, was produced in this way. It arose from a cross that is usually referred to as a double cross. One of its parents is a selection from a cross between Marquis and Iumillo (a resistant durum variety), the other a selection from a cross between Marquis and Kanred (a partially resistant winter wheat). Part of the resistance of Thatcher, therefore, came from Iumillo and part from Kanred.

Many of the wheats grown in Canada and the United States in the period from 1937 to 1950 possessed a type of resistance known as "mature-plant resistance". These varieties (for example, Regent, Redman, Mida, Cadet), as they grow towards maturity, gradually develop a type of resistance that, until the advent of race 15B, proved effective against all stem-rust races prevalent in the wheat-growing areas of North America. This type of resistance, which proved so valuable for many years, was derived from an emmer wheat, known as Yaroslav Emmer. By crossing this variety with Marquis, Mr. E. S. McFadden, at Brookings, South Dakota, succeeded in transferring its resistance to two new varieties, Hope and H-44-24. Neither of these wheats proved to be commercially valuable, but most of the rust-resistant North American wheats grown before 1950 derived their rust resistance from them.

The discovery and subsequent widespread outbreak of Race 15B and the measures taken in breeding a bread-wheat variety resistant to it, provide a good example of how plant breeding functions as a means of rust control. This race was discovered about 1940. Soon thereafter studies on its infective abilities made it apparent that, if it ever became widely distributed, it could severely damage all the most useful bread-wheat and durum-wheat varieties grown at that time in North America.

Before plant breeding could even be attempted, it was necessary to discover a source of resistance against Race 15B. Such resistance was found in the variety McMurachy (named after the Manitoba farmer who selected it). This wheat

did not have the agronomic, milling, and baking qualities required for a commercial wheat, nor the necessary resistance to leaf rust, but it did have resistance to Race 15B and the various other stem-rust races then known to occur in North America. Since it was desired to produce a commercial wheat resistant to leaf rust as well as stem rust, McMurachy was crossed with the leaf-rust-resistant variety Exchange. The resulting hybrid lines had the necessary stem-rust and leaf-rust resistance but, because both parents were poor in quality, the hybrids lacked the quality required in a commercial wheat. This quality was obtained by crossing the hybrids repeatedly with the variety Redman and retaining only those new hybrid lines that had the highest quality combined with the necessary rust resistance. The ultimate product of this series of crosses was the variety Selkirk, which was released to farmers in the spring of 1954.

When breeding for rust resistance in oats was undertaken in Canada, no varieties were known that had resistance to all races of oat stem rust in North America. The best that could be done at the time was to produce varieties resistant to the most common races of the rust (Races 1, 2, and 5), which accounted for about 95 per cent of oat stem rust present in Canada each year. The varieties Vanguard and Ajax, released in 1937 and 1942, respectively, were resistant to the common races and could, therefore, be expected to remain practically free from rust so long as rarely occurring races, such as Races 6 and 8, did not increase. The first notable increase of a race that could damage these varieties took place in 1943, when Race 8 began to appear rather commonly in the Prairie Provinces. Since then this race gradually increased until, five years later, it made up almost half of the oat stem rust present in Canada. The increased prevalence of Race 8 has caused Vanguard, Ajax, and other varieties with similar resistance to rust considerably, but these varieties suffer less from rust than older varieties susceptible to all races.

To cope with the possible increase of Race 8, plant breeders in the United States produced such varieties as Clinton, Mindo, and Bonda, which possess resistance to this race and to the common races as well. These varieties, however, lacked resistance to Races 6 and 7. Consequently, an increase of these races would endanger this type of variety. A sudden increase of Race 7 in 1950 showed that the resistance of these varieties could not be depended on. Therefore, the objective of producing an oat variety resistant to all known oat stem rust races became imperative. This objective was achieved at the Cereal Breeding Laboratory, Winnipeg, by the production of the variety Garry, which is not only resistant to the known races of oat stem rust but has resistance also to many races of crown rust.

It is clear from the foregoing discussion that the rust-resistant cereal varieties produced from time to time are not likely to remain rust-resistant permanently. It is possible that a variety with permanent rust resistance may be produced, but it is not possible to predict, at the time of its distribution, that its resistance will be permanent.

The difficulty of producing varieties with permanent disease resistance is a consequence of the tremendous variability that exists in most disease-producing organisms. Owing to this variability most microorganisms, including the rusts, are made up of numerous strains or races. When a new cereal variety is produced, the most that the rust investigator can say for it is that it is resistant to all *known* races of a rust. That is not to say that it is resistant to *all* existing races, because some races, unknown to the investigator, are likely to exist in small quantities and may be able to attack the new variety. If these races exist in, or are introduced into, the area in which the new variety is grown, they are likely to increase greatly in a few years.

The most important function of the investigator of the rusts is to discover the presence of new and dangerous rust races before they become widely distributed and so be able to warn the plant breeder that danger lies ahead. Breeding can then be undertaken against the threatening race in order that the production of resistant varieties will have progressed as far as possible before the new race becomes sufficiently prevalent to be destructive to the varieties then being grown. Breeding of oats resistant to Races 8 and 7 of oat stem rust was attempted while these races were still scarce. Breeding of a wheat resistant to Race 15B was undertaken five years before that race became prevalent in the great wheat-growing areas.

As races of rust can sometimes increase very rapidly and, as it requires about 10 years to produce a new cereal variety, the plant breeder may occasionally lose out in the race with the rust. But if the surveys for the presence of new rust races are performed effectively, and if resistant breeding material can be found quickly enough, the farmer should never, for long, remain without a rust-resistant variety.

Perhaps the most encouraging development in rust research work in recent years is the international co-operation set in motion after the outbreak of Race 15B of wheat stem rust in 1950. Before that time there had been a certain amount of co-operation of an informal nature between individuals or institutions in several countries. At a meeting held at St. Paul, Minnesota, in November, 1950, co-operation in rust research, at least for North and South America, was placed on an organized basis. In consequence, "rust nurseries," that is, experimental plots for testing the resistance of cereal varieties under severe rust conditions, have been established in Canada, the United States, Mexico, and several South American countries. The great World Collection of more than 12,000 wheat varieties maintained at Washington, D.C., is gradually being tested in these rust nurseries and in the greenhouses of a number of laboratories in order to discover the varieties with most rust resistance. Hybrid wheats from plant-breeding laboratories in Canada and other countries are tested in these nurseries to determine their rust resistance, and are also tested in certain laboratories for their reaction to known rust races. Attempts are being made to introduce into wheat varieties additional rust resistance from rye and from certain grasses that are related to wheat. When any Canadian hybrid wheats are found to show promise as possible new varieties, they are increased as rapidly as possible, in the summer in Canada and in the winter in southern California. For the first time in history, the available resources of science are being fully used to provide rust-resistant varieties of cereals.

SUMMARY

Stem rust is a destructive and widespread disease of cereals. It is caused by a fungus with a rather complex life cycle. Two stages of this cycle, the red and the black, occur on cereals and grasses, a third stage occurs on barberry.

Spores of the red stage are readily distributed by wind. They germinate when moisture conditions are favorable, and infect cereals and grasses. Each infection gives rise to a pustule containing numerous spores. Under favorable conditions, a new generation of red spores is produced each week, so that the disease increases very rapidly. Only in mild climates is the red stage able to persist from one season to the next.

When infected cereal or grass plants begin to ripen, the fungus ceases to produce red spores and, in their place produces black (winter) spores. These spores remain attached to the plants on which they are produced and are not, therefore, readily distributed by winds. They cannot infect cereals or grasses. They can withstand severe cold, but they are less successful in withstanding prolonged exposure to high temperatures. They require about a six-month period of dormancy before they will germinate. The black spores are, therefore, adapted to survive winter conditions.

After their dormancy period, that is to say, in the spring, the black spores readily germinate whenever temperature and moisture conditions are suitable. On germination, they give rise to spores of a totally different type, called sporidia. The sporidia are distributed by wind. They are not able to infect cereals or grasses, but, if barberry is growing in the vicinity where they are produced, they infect its young leaves and twigs. Such infections give rise on barberry to the cluster-cup stage of the fungus. In the cluster cups (aecia) another type of spore called aeciospore is produced. These spores, too, are distributed by winds. If they lodge on green susceptible cereal or grass plants, they infect them, and thus complete the life cycle of the fungus.

There are several varieties of stem rust. They are very similar in appearance, and are distinguished from one another by the host plants that they are able to infect. For example, one variety infects wheat and barley but not oats, another infects oats but not wheat or barley. Three varieties—wheat stem rust, oat stem rust, and rye stem rust—are known to comprise a number of different races. The races of wheat stem rust are distinguished by their ability to attack certain wheat varieties; those of oat stem rust, by their ability to attack certain oat varieties; and those of rye stem rust, by their ability to attack certain varieties of rye.

The fungus has a sexual stage, which begins when the black spores germinate. The sporidia produced are of two sexes. The sexual stage is completed on barberry. It is possible, therefore, for varieties and races of stem rust to hybridize on barberry and produce new races.

To control stem rust, the most effective method is to grow resistant varieties. Other methods consist in the destruction of barberry, the sowing of early-maturing varieties, the securing of early maturity by cultural practices, and the use of chemicals.

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